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ACCELERATING FISHES INCREASE PROPULSIVE EFFICIENCY BY MODULATING VORTEX RING GEOMETRY.

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Abstract

Swimming animals need to generate propulsive force to overcome drag, regardless of whether they swim steadily or accelerate forward. While locomotion strategies for steady swimming are well characterized, far less is known about acceleration. Animals exhibit many different ways to swim steadily, but we show here that this behavioral diversity collapses into a single swimming pattern during acceleration regardless of the body size, morphology, and ecology of the animal. We draw on the fields of biomechanics, fluid dynamics and robotics to demonstrate that there is a fundamental difference between steady swimming and forward acceleration. We provide empirical evidence that the tail of accelerating fishes can increase propulsive efficiency by enhancing thrust through the alteration of vortex ring geometry. Our study provides new insight into how propulsion can be altered without increasing vortex ring size, and represents a fundamental departure from our current understanding of the hydrodynamic mechanisms of acceleration. Our findings reveal a unifying hydrodynamic principle that is likely conserved in all aquatic, undulatory vertebrates.

Significance Statement

The ability to move is one of the key evolutionary events that led to the complexity of vertebrate life. The most speciose group of vertebrates, fishes, displays an enormous variation of movement patterns during steady swimming. We discovered that this behavioral diversity collapses into one movement pattern when fishes are challenged to increase their swimming speed, regardless of their body size, shape and ecology. Using flow visualization and biomimetic models, we provide the first mechanistic understanding of how this conserved movement pattern allows fishes to accelerate quickly.

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Introduction

Over the course of evolutionary time, patterns of animal locomotion have diversified to take advantage of the physical environment through the interplay of morphology, physiology and neural control. Yet, two fundamental principles of locomotion in most animals remain the same: 1) Force is generated by transferring momentum to the environment through repetitive motions such as body undulations and oscillating appendages (legs, fins, or wings), and 2) the locomotor speed is modulated by controlling the amplitude and frequency of these periodic motions (1, 2). Previous studies have demonstrated that the degrees of freedom in amplitude and frequency control are not limitless, but rather constrained by the physical laws imposed by the environment. For example, flying animals must maintain a high wing-beat frequency to generate enough lift, controlling speed primarily by altering the wing's angle of attack(3). In contrast, the morphology and locomotion strategies of aquatic animals have adapted to moving through a viscous environment where gravitational forces are negligible. Among these strategies, the ancestral state of aquatic locomotion is axial undulation, where muscle contractions bend the body into a mechanical wave that passes from head to tail (4). The interaction of angled body surfaces with the surrounding fluid propels the animal forward, and the movements of the entire body contribute to the overall swimming performance (5-10).

Over the past several decades, a number of studies have investigated the kinematics (11-14), muscle activity (15-18) and hydrodynamics (19-21) of tail movements, in particular how tail beat amplitude and frequency are controlled during steady swimming. Most undulatory vertebrates such as fishes, alligators, dolphins and manatees control speed by primarily modulating tail beat frequency while maintaining a relatively low tail beat amplitude (22-25). At high steady swimming speeds, tail beat amplitude reaches a plateau at around 0.2 body length

(*L*). Computational studies (26-29) and experiments with hydrofoils (30, 31) suggest that swimming animals operate in this range to maintain high swimming efficiency.

How do these mechanisms apply when a steadily-swimming animal accelerates forward, which is often used to catch prey, avoid predators or save energy during migrations (32, 33)? One hypothesis is that speed is gained only by further increasing the tail beat frequency (34-37). Alternatively, an animal can bend its body maximally to accelerate large amounts of fluid, as seen in Mauthner initiated C-starts (38-41). Yet emerging studies suggest that forward acceleration exhibits distinct kinematics (42-46) that defy both hypotheses, indicating that acceleration may have its own optimization strategy. Although forward acceleration has been a topic of interest for decades in the field of aquatic locomotion (39, 43), a comprehensive understanding of its prevalence and underlying mechanisms has remained elusive. Here, we identify a new undulatory locomotion strategy for forward acceleration by integrating complementary approaches: biological experiments with live fishes and physical experiments with bio-mimetic fish models.

Results and Discussion

Acceleration kinematics across fish phylogeny

We discovered that in fishes tail beat amplitude is consistently higher during acceleration than during steady swimming (Fig. 1). This pattern is conserved across 51 species examined, with representatives from a wide range of phylogenetic positions from chondrichthyes (e.g. bonnethead shark, *Sphyrna tiburo*) to tetraodontiformes (e.g. stripped burrfish, *Chilomycterus schoepfi*). These species exhibit vastly different body shapes, ecological habitats and swimming modes (Table S1). Some species use median or pectoral fins during steady swimming (e.g. clown knifefish, *Chitala ornata* and sergeant major, *Abudefduf saxatilis*), but always revert to body undulation when they accelerate forward from steady swimming.

When we plot tail beat amplitude during acceleration against steady swimming for all species, we found that the relationship is linear (Fig. S1a). This suggests that the relative increase in tail beat amplitude during acceleration is constant at 34±4%. However, there is substantial variation in the absolute amplitude values that depends on body length and shape. For example, when body length is held constant, elongate fishes such as Florida gar (*Lepisosteus platyrhincus*) and Northern barracuda (*Sphyraena borealis*) accelerate with lower tail beat amplitudes (0.19±0.01 *L*) compared to more fusiform fishes such as tarpon and red drum (0.24±0.01 *L*). We also found that during acceleration tail beat amplitude decreases with body length (Fig. S1b).

To better understand if there is a common propulsive strategy across fish diversity, we next performed a more detailed midline analysis of the entire body during steady swimming and forward acceleration for 9 species. Despite extreme differences in body shape and swimming mode, we found that all fishes share similar midline acceleration kinematics. These acceleration bouts are usually brief, typically less than five tail beats. All points along the body show higher

amplitudes compared to steady swimming, but not as high as seen during C-starts (39, 40) (Fig. S2-4). Further analyses on the travelling body wave and tail movement suggest efficient force production during acceleration (Table S2). The average values across 10 species for slip ratio, Strouhal number (St) and maximum angle of attack (α_{max}) are 0.80±0.02, 0.41±0.01, and 22.71±0.65˚, respectively. Slip ratios approaching 1 reveal high swimming efficiency, while experiments with thrust-producing, harmonically oscillating foils show that propulsive efficiency is maximized when St falls within the range of 0.2 and 0.5 and α_{max} is between 15˚ and 25˚ (30).

In addition to the species studied here, similar acceleration kinematics was previously observed in American eels (44). These elevated amplitudes are most notable around the head and tail. The onset of acceleration (which can be easily recognized because of strong head yaw and a faster tail beat) provides a reference point to interpret the phase relationship between head and tail. By doing so, we found that the motion of the head always precedes the motion of the tail, indicating that the body wave is initiated by strong head movements in all species, though the timing between head and tail movements is not constant. To more closely investigate the kinematics and hydrodynamics of acceleration, we chose a generalized teleost fish, the rainbow trout (*Oncoryhnchus mykiss*). The swimming kinematics of this species has been studied in great detail for steady swimming and other behaviors but not for acceleration (5, 13, 47-54). Like other species tested in this study, the body amplitudes of trout are higher during acceleration than during steady swimming (Fig. S5a), and head movements precede the motion of the tail (Fig. S5b).

We next examined how swimming speed and acceleration depend on tail beat amplitude, given that a range of amplitudes is evident for each behavior (Fig. S5c). As others have shown previously (44), we found that in general tail beat frequency, not tail beat amplitude, has the

most effect during both behaviors (Fig. S5d). Multiple regression analysis revealed that steady swimming speed increases only with tail beat frequency. This trend is similar during acceleration, though tail beat amplitude also has a minor effect (Table S3). Our results suggest that tail beat amplitude does not change during steady swimming or acceleration, but jumps discretely by ~30% when fish transition from one behavior to another. Thus, trout appear to have two undulatory gears based on tail beat amplitude; one for steady swimming and another for acceleration. Our results suggest that this discrete jump in tail beat amplitude during acceleration is correlated with increased head yaw (Fig. S5e), and these movements are tightly phase-locked, with the head preceding the tail (Fig. S5f).

Hydrodynamic effects of increased tail beat amplitude during acceleration

We next investigated how increased tail beat amplitude relates to thrust production and propulsive efficiency by using a combination of quantitative flow visualization experiments on live fish and experiments with actuated, soft-bodied robotic models. Results from particle image velocimetry show that fish can reach a maximum acceleration rate of 20 L s^{-2} from initial swimming speed of 3 L s^{-1}. To accomplish this, fish transfer more axial momentum to the fluid by generating stronger vortices compared to steadily swimming fish (Fig. 2a). Similar wake structures were previously observed in zebrafish (55), eel (44) and carp (45). In addition, fish entrain more fluid around their posterior body to strengthen shed vortices (Fig. 2b). This occurs because the posterior body has a greater curvature, which creates a low pressure region in the concavity (Fig. 2b, t=12.5 ms). The entrained fluid in this low pressure region (blue) follows the traveling body wave until it reaches the trailing edge of the tail (t=50 ms). At the point when the tail reverses direction, the fluid starts to roll off the tail and into the wake (t=56.3 ms).

Concurrently, the body concavity causes flow to build up on the opposite side. This fluid (red) starts getting released to the wake as the tail increases its velocity (t = 68.8 ms). When the tail reaches its maximum velocity a vortex is formed (t=81.3 ms), owing to the occurrence of two bodies of fluid moving in opposite directions. Our results indicate that during acceleration body undulations of trout are responsible for increased wake velocity and vorticity. This is not surprising as multiple studies have shown that body-induced flows can enhance vortex shedding in other species (7, 8, 10, 19, 56, 57).

When fish swim, they generate vortex rings (58-60). We see this in two dimensions as two counter-rotating vortices (i.e. vortex cores) in the wake after each tail beat (61-63). In recent years, estimating locomotive forces from wake measurements has garnered much interest with hopes of better understanding the resultant motion of the animal (41, 56, 64-66). Several methods have been proposed to estimate locomotive forces (56, 64, 67, 68). The one which we used in this study is based on the classical vortex ring theory (69). We calculated the impulse (i.e. the average force) applied to the fluid during each tail beat by measuring the circulation, jet angle (θ), core diameter (D_o) and the spacing between the two vortex cores (D). We found that an accelerating trout generates an impulse (along the swimming direction) that is at least 4 times higher than that required for its initial steady swimming speed (Fig. 2c). This higher impulse is due to 172 ±16% increase in vorticity. In addition, the jet angle is oriented ~30±3% more downstream, which devotes a greater proportion of the impulse along the swimming direction.

We found that D is reduced by ~25% from 0.33 L to 0.25 L when fish transition from steady swimming to acceleration. At first glance this may be surprising given that the impulse and kinetic energy of a ring is proportional to its size. However, impulse and energy also depend on the geometry of the vortex ring itself. One key parameter of the ring geometry is the ratio

between minor and major axis diameters (d/D). When d/D approaches one, the ring becomes more axisymmetric, which is favorable because axisymmetric rings possess the maximum amount of energy relative to other shapes that maintain the same total impulse (70, 71). Given that d is always constrained by the span of the tail (7, 58, 59, 62, 72), the axisymmetry of the ring primarily depends on D. Our results show that during steady swimming trout generate elliptical rings (d/D=0.66). In contrast, we found that during acceleration the geometry of the vortex rings become more axisymmetric (d/D=0.88).

The impulse of a vortex ring is also proportional to the ratio of its core diameter to its ring diameter (D_o/D). In addition to having a more axisymmetric shape, we found that the vortex rings generated by accelerating trout have thicker cores (D_o/D=0.37±0.02) than those generated by trout swimming steadily (D_o/D=0.25±0.01). It has been shown that for vortex rings generated by a piston pushing a cylinder of fluid through a nozzle there is a limit in generating thicker arms efficiently, because at some point (piston stroke to diameter ratio>3.5) separation occurs and energy dissipated by a trailing edge of fluid (73-75). For finite-core, axisymmetric vortex rings which propagate steadily (76), this piston stroke to diameter ratio corresponds to D_o/D = 0.42 in a vortex ring (77, 78). Perhaps not coincidentally, the vortex rings generated by accelerating trout have D_o/D close to 0.42. In order to evaluate whether our fish-generated vortex rings during acceleration can be compared to nozzle-generated rings, we analyzed their velocity and vorticity distributions along a center line connecting the two vortex cores, and confirmed that they closely match the values reported for nozzle-generated rings (73, 79) (Fig. S6a-c). In addition, we investigated the temporal dynamics of vortex rings once they are shed into the wake, and found that they translate downstream with a constant velocity while preserving their D_o/D ratio (Fig.

S6d). What this suggests is that the hydrodynamic principles of efficient thrust production in oscillating fish may be similar to those observed during biological jet propulsion (65, 80-82).

Overall, our findings indicate that accelerating trout generate more thrust, not by generating larger rings but, by modulating their geometry and orientation. To investigate how common this phenomenon is, we analyzed d/D, D_o/D and θ of four additional species with different swimming modes and body shapes and found similar results (Table S3). In addition, flow imaging on a similar sized American eel (L=23 cm) shows that during acceleration anguilliform swimmers also generate vortex rings with comparable D_o/D ratio (~0.4 based on Fig. 1b in (44)). It remains to be seen, however, how D_o/D ratio scales with body size, given that it is significantly higher (0.6-0.7) for smaller fish such as zebrafish (83) and koi carps (45). Note that a 2-dimensional geometric analysis of vortex rings provides an initial, albeit qualitative understanding on how fishes accelerate efficiently. Concatenated, ring-like structures involved in the wakes of fishes can be highly elongated and 3-dimensional, and may not have the same properties (e.g. momentum, energy, and stability) as nozzle-generated rings.

Relationship between tail kinematics and vortex ring geometry We next propose a set of equations to provide a mechanistic understanding of how the geometry (d/D and D_o/D) and angle (θ) of a vortex ring depend on the tail kinematics. Because the oscillating tail generates each core of a vortex ring successively, we used trigonometric relations to define $D = \sqrt{a^2 + b^2}$ and $\theta = \tan^{-1}\left(\frac{a}{b}\right)$, where a and b are the vertical and horizontal spacing between the two cores, respectively. Based on our wake analysis, the vertical spacing depends on the tail beat amplitude (i.e. a = half of the tail beat amplitude), and the horizontal spacing depends on the tail beat frequency and swimming speed (i.e. b = swimming speed multiplied by half tail beat cycle). To

validate our approach, we calculated D and θ for trout swimming steadily at 3 L s^{-1} and accelerating from the same initial speed. During acceleration we assumed that the swimming speed was 4 L s^{-1} (i.e. the average between initial and final swimming speeds). We compared the predicted D and θ to those measured experimentally, and found a good match (Fig. 2D, D=0.31 L and θ=75.07° during steady swimming and D=0.22 L and θ=63.43° during acceleration).

Once we validated our approach, we used it to further investigate the contribution of increased tail beat amplitude during acceleration. We computationally explored an alternative scenario where the tail beat amplitude was kept constant at the value observed for steady swimming (0.16 L), and speed was gained by further increasing the tail beat frequency (i.e. hypothetical acceleration). Given that thrust is proportional to the square of tail beat frequency multiplied by the square of tail beat amplitude (84, 85), we increased the tail beat frequency from 10 Hz to 12.5 Hz in order to maintain the same effective thrust. We found that this had no effect on the ring angle (θ=63.43°), but generated a suboptimal D=0.18 L with d/D=1.22 and D_o/D=0.56 (we assumed that d=0.22 L and D_o=0.1 L). Therefore, we believe that the increase in tail beat amplitude observed in trout is the key to geometrically generating the most efficient rings.

<u>The swimming performance of robotic models increases with tail beat amplitude</u>

While it is favorable to generate more thrust by producing vortex rings with optimal geometry, this does not reveal the overall swimming efficiency of an accelerating fish because motions that produce them may be costly. It is not unreasonable to imagine that large lateral body amplitudes would incur large drag penalties (44, 45). To resolve this tradeoff, we employed experiments with a biomimetic trout model to systematically explore how different tail beat amplitudes affect steady swimming and acceleration performance (Fig S7). This level of

256 experimental control is impossible to achieve with live fish. We generated undulatory
257 movements in our flexible fish model from a single actuation point located just posterior to the
258 head. Therefore, we were able to control tail beat amplitude by modulating the head yaw.

259 We first measured performance during steady swimming and acceleration at yaw
260 amplitudes very similar to those of live fish (10° and 20°). We found that during steady
261 swimming the model performed better when it is actuated with smaller yaw (Fig. S8a). However,
262 during acceleration this relationship is reversed; swimming performance is consistently higher
263 with larger yaw (Fig. S8b). This suggests that there is no convergence of optimum head yaw
264 between steady swimming and acceleration. While steady swimming seeks to preserve
265 momentum by streamlining motions, during acceleration additional momentum must be
266 generated despite drag costs.

267 To determine if there are yaw values that maximize swimming efficiency during
268 acceleration, we measured efficiency at yaw amplitudes between 0° and 30° at 3° increments.
269 We found that efficiency increases linearly with yaw amplitudes up to 20°, beyond which values
270 plateau (Fig. 3). When we map head yaw from live fish onto our model performance curve, we
271 found that increasing head yaw from steady swimming values to acceleration values can create
272 an increase in efficiency up to 100%. It is perhaps no accident that the yaw amplitudes chosen by
273 accelerating fish fall within the range that gives greatly increased propulsive efficiency compared
274 to steady swimming. We hypothesize that this is due to generating hydrodynamically more
275 efficient vortex rings, based on our flow measurements in the wake of live fishes. However,
276 increasing head yaw to accelerate with more optimal vortex rings does not mean that producing
277 these rings costs less than the rings produced during steady swimming (Figure S9 shows a 50%
278 increase in mechanical power input for increased head yaw).

The ability to move is one of the key evolutionary events that led to the diversity and complexity of vertebrate life. Given that movement through fluids is energetically costly, fishes have found many ways to minimize drag during normal, steady swimming, such as keeping the body straight and using median or paired fin locomotion (86-88). While steady swimming is optimized for endurance by minimizing the energetic investment, acceleration favors maximizing force production to escape quickly from predators or capture elusive prey. Here, we show that the enormous behavioral diversity observed during steady swimming collapses into a single locomotion strategy when fishes transition to forward acceleration. We believe that this strategy is likely conserved across all undulatory swimmers and not just fishes because it is hydrodynamically the optimal solution to maximize propulsive efficiency.

Methods

All research protocols were approved by the Institutional Animal Care and Use Committee at the University of Florida. All data analyses were performed in Matlab (Mathworks) and all values are shown as mean ± standard error of the mean, unless stated otherwise.

Diversity of swimming kinematics across species Our data set included 51 species of salt and freshwater fish (105 individuals, from 20 taxonomic orders), which were either obtained from commercial dealers or wild caught using cast net or hook-and-line. The details about these species are given in Table S1, and the research protocols are described in Text S1.

Swimming hydrodynamics of rainbow trout We used digital particle image velocimetry to quantify the flow fields around and behind steady swimming and accelerating trout. We estimated wake forces as described in (66) (see Text S2 for more details on the experimental procedures and data analysis).

Experiments with the physical fish model We performed the experiments in the flow tank at Harvard University which is customized to house a computer-controlled external actuator. We used this system in the past to evaluate the swimming performance in a number of swimming mechanical models (5, 89-91). Here, we systematically moved the physical model with different tail kinematics and measured the total sum of forces acting on the whole body. For these

311 measurements, we calculated the propulsive force produced by the model and the corresponding
312 power output of the actuator as described in (92) (see Text S3 for more details).

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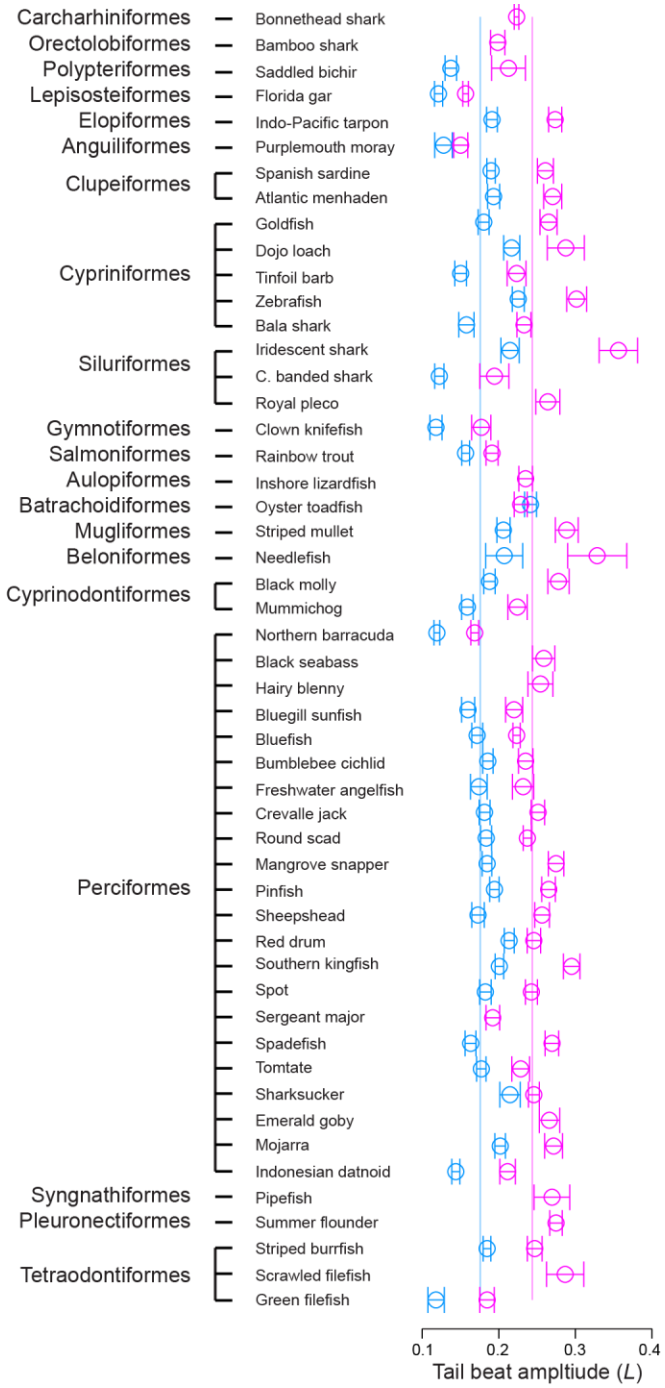
Figures

Figure 1



536 Figure 2.

537

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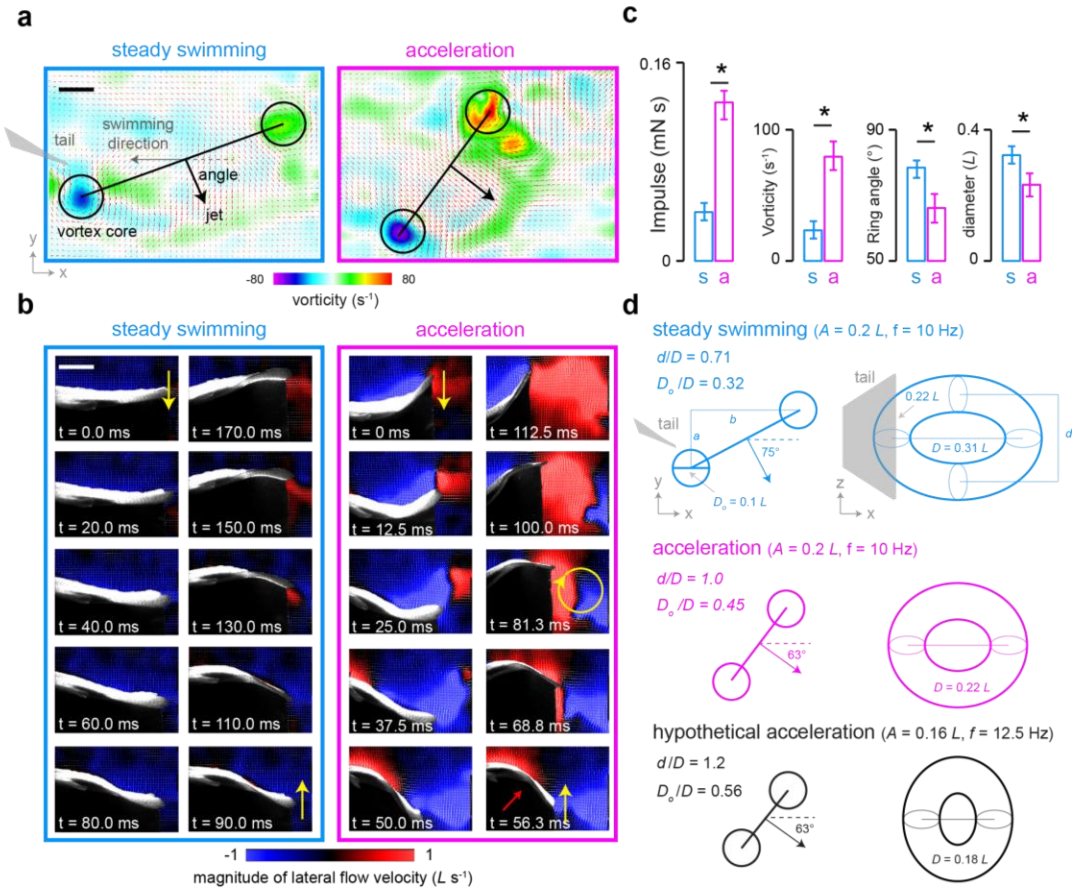
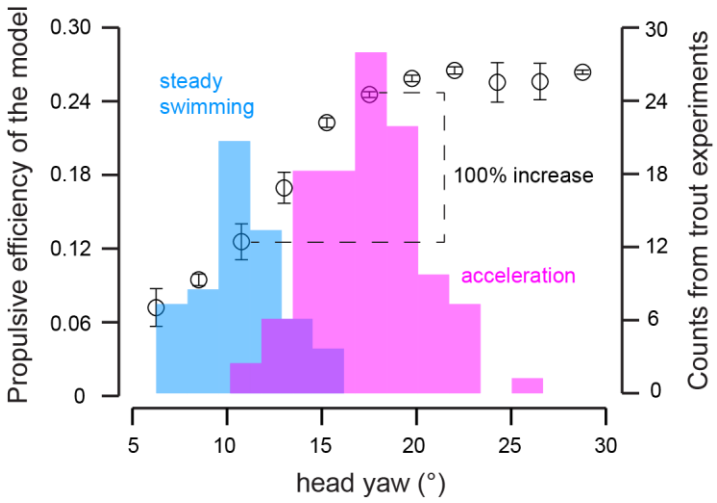

a
steady swimming
acceleration
tail
swimming direction
angle
jet
vortex core
y
x
-80
80
vorticity (s⁻¹)
b
steady swimming
acceleration
t = 0.0 ms
t = 170.0 ms
t = 20.0 ms
t = 150.0 ms
t = 40.0 ms
t = 130.0 ms
t = 60.0 ms
t = 110.0 ms
t = 80.0 ms
t = 90.0 ms
t = 0 ms
t = 112.5 ms
t = 12.5 ms
t = 100.0 ms
t = 25.0 ms
t = 81.3 ms
t = 37.5 ms
t = 68.8 ms
t = 50.0 ms
t = 56.3 ms
-1
1
magnitude of lateral flow velocity (L s⁻¹)
c
0.16
Impulse (mN s)
0
100
Vorticity (s⁻¹)
0
90
Ring angle (°)
50
0.4
diameter (L)
0
s a
d
steady swimming (A = 0.2 L, f = 10 Hz)
d/D = 0.71
D_o/D = 0.32
tail
a
b
75°
D_o = 0.1 L
0.22 L
D = 0.31 L
d
acceleration (A = 0.2 L, f = 10 Hz)
d/D = 1.0
D_o/D = 0.45
63°
D = 0.22 L
hypothetical acceleration (A = 0.16 L, f = 12.5 Hz)
d/D = 1.2
D_o/D = 0.56
63°
D = 0.18 L

539
540

541 Figure 3.



542

Figure Legends

Figure 1. Fishes have higher tail beat amplitude during acceleration. (a) This phenomenon was confirmed across a wide range of fishes from 20 taxonomic orders with different body shapes, swimming modes and ecologies. Blue and magenta lines indicate the mean tail beat amplitudes for steady swimming (0.181 ± 0.004 *L*) and acceleration (0.244 ± 0.006 *L*), respectively. Mean tail beat amplitudes for steady swimming and acceleration are statistically different (unpaired T-test, $P<0.001$). During steady swimming, it was not possible to measure the tail beat amplitude of few species (black seabass, sergeant major, pipefish, summer flounder and filefish), as they use primarily median or pectoral fins for propulsion. Error bars are ± one standard error of the mean.

554 Figure 2. Hydrodynamics of steady swimming versus acceleration. (a) Representative flow fields
555 behind a rainbow trout (L=32 cm) swimming steadily at 3 L s^{-1} (left) and accelerating (right)
556 from the same initial speed. The heat map denotes vorticity where negative (magenta) and
557 positive (red) values indicate clockwise and counter-clockwise rotation, respectively. The length
558 of the scale bar is 2 cm. (b) Body movements of the same fish during steady swimming (left
559 column) and acceleration (right column) over one representative tail beat cycle. Yellow arrows
560 indicate the direction of tail movement. The blue and red denote the magnitude of left and right
561 flow fields, respectively, in the fish frame of reference. In each video frame, the body of the trout
562 is visible from the dorsal fin to the tail, which represents the 30% of the total length. The length
563 of the scale bar is 4.5 cm. (c) Mean impulse, vorticity, angle and diameter of an average vortex
564 ring for steady swimming and acceleration (10 tail beats from each fish, n=2 fish). * denotes
565 significant at P<0.01, unpaired T-test. Error bars are ± one standard error. (d) Hypothesized
566 vortex ring geometry and orientation behind fish swimming steadily (blue) and accelerating
567 (magenta). Hypothetical acceleration with lower tail beat amplitude is also shown for
568 comparison (black).
569

570 Figure 3. Fishes adopt acceleration kinematics tuned for high propulsive efficiency. Propulsive
571 efficiency of the physical model as a function of head yaw at flow speed 1.2 L s^{-1} (left axis, black
572 points; error bars are ± one standard error); propulsive efficiency increases with increasing head
573 yaw. A histogram of head yaw (right axis) is shown for live trout during steady swimming (blue)
574 and acceleration (magenta). Note that the overlapped region between the distributions steady
575 swimming and acceleration appears darker. The average head yaw for steady swimming and
576 acceleration is 12.469± 0.370° and 17.805±0.352°, respectively (unpaired T-test, P<0.01).
577